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POSEIDONEMERTES COLLARIS, N.SP. (NEMERTEA: AMPHIPORIDAE) FROM CALIFORNIA, WITH NOTES ON ITS BIOLOGY

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Abstract.—The morphology of a new monostiliferous hoplonemertean, *Poseidonemertes collaris* (Amphiporidae) from Bodega Harbor, California, is described and aspects of its biology are discussed. Anterior musculature and other characteristics are those of the genus. Diagnostic specific features include a readily-contracted, pointed head, two eyes, and branched intestinal diverticula.

Specimens of a small, rather common nemertean were collected from intertidal areas of Bodega Harbor, Bodega Bay, California. Although the fauna of this area is relatively well-known, this worm was previously undescribed. Externally, the animal closely resembles a number of other small, whitish, two-eyed nemerteans. Examination of its internal structure, however, reveals it to be a new species in the genus *Poseidonemertes*.

Materials and Methods

Between June 1980 and June 1982, 23 specimens were obtained from 193 samples (200–500 cc^3 each) of surface sediments in Bodega Harbor, California. Other individuals were obtained from less quantitative sampling. The samples of sediment were washed and sorted by hand in shallow trays, and the nemerteans were removed. External morphology and some internal features were observed in living animals. Specimens were anesthetized in 7% $MgCl_2$, fixed in sea water Bouin, embedded in paraffin, cut in 10 μm sections and stained in Ehrlich's hematoxylin and eosin.

Poseidonemertes collaris, new species
Figs. 1–11

Type-material.—The following have been deposited at the National Museum of Natural History (Smithsonian Institution):

Holotype: Entire specimen, preserved in 5% formalin, collected 5 Nov 1982, length 22 mm, width 13 mm, USNM 80917.

Paratype: A complete set of transverse sections of a male, USNM 80918.

Type-locality.—Bodega Harbor, Bodega Bay, Sonoma County, California (38°18′N, 123°2′W) in intertidal muddy sand.

Etymology.—Named for the characteristic behavior of drawing the tip of the head into the body, forming a collar of tissue around the retracted head.

Diagnostic characteristics.—Body stout, approximately 20 mm × 1.2 mm; sharply pointed anterior head region; 2 conspicuous ocelli nearly terminal; color in life ivory to apricot; rhynchocoel full length of body, proboscis at least ¾ body

length; body wall longitudinal muscles divided anteriorly, inner and outer layers forming proboscis insertion; cephalic retractor muscles from inner longitudinal layer; body wall diagonal muscle layer present; intestine with unbranched caecum and bifurcated lateral diverticula.

Additional material examined.—Three series of transverse sections, 2 series of frontal sections, 2 series of sagittal sections including both males and females, plus several living animals.

External features and behavior.—Twenty measured living animals ranged in length from 7.5 mm to 37 mm (average = 20.4 mm, SD = 6.9, N = 20) and width from 0.7 mm to 2 mm (average = 1.2 mm, SD = 0.37, N = 18) when crawling. Color ranges from ivory to nearly apricot. In some specimens intestinal diverticula appear gray-green or greenish-yellow. The epidermis of some individuals contains white or brown pigment spots or granules scattered over the body.

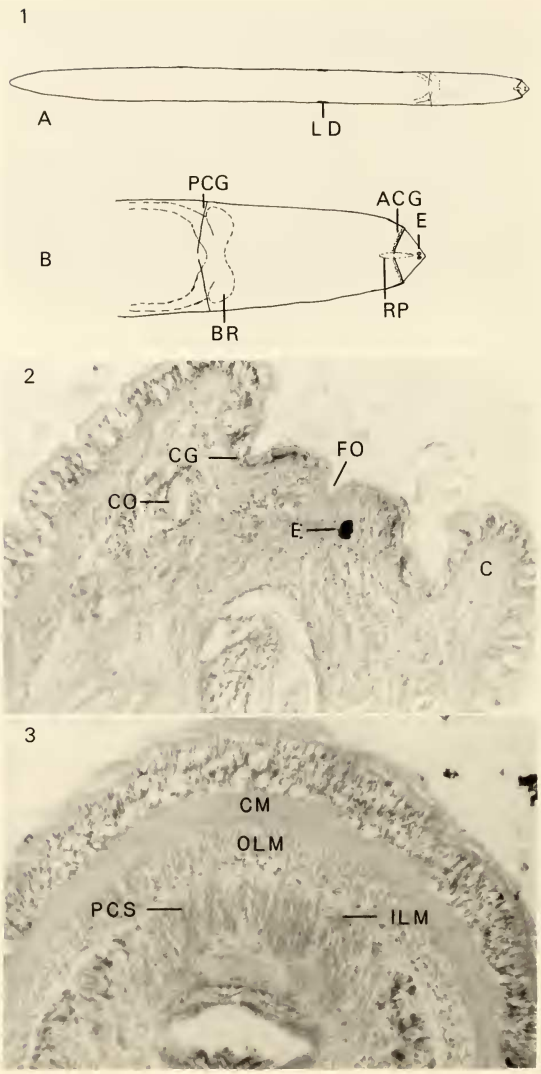
Animals tend to be stout, with the posterior end often broader than the anterior. They are highly contractile, and can easily shorten to ⅓ or ¼ their expanded length. When contracting, worms do not coil or twist, and the head remains pointed. Two large, prominent eyes are located close together near the tip of the head (Fig. 1). Pigment cups of the eyes are comma to round in overall shape. Two pairs of cephalic grooves are present. The anterior pair is distinct, both dorsally and ventrally, is far anterior to the brain, and is sometimes united dorsally. The anterior cephalic grooves vary in shape. They usually form a posteriorly directed chevron, although they can form a transverse or even an anteriorly directed curve across the head. On the dorsal surface of the head, the anterior cephalic grooves are often bordered by reddish-brown pigment spots (Fig. 1). Along the lateral margins of the head, a groove extends from the anterior cephalic grooves a short distance posteriorly. The distance from the tip of the head to the anterior cephalic groove is about 0.2 mm. Living animals frequently and characteristically retract the head to the level of the anterior cephalic grooves, forming a collar of epidermal tissue around the tip (Fig. 2). We were unable to relax animals before fixation to the point that the collar did not form. The posterior cephalic grooves, just posterior to the brain, are thin, fine lines not highly visible (Fig. 1).

The brain lies far behind the anterior cephalic grooves, the distance being about 1.5 mm in one animal measured. The brain and anterior parts of the lateral nerve cords appear light pink when viewed through the body wall. Gonads are not readily visible through the rather opaque epidermis.

In living specimens a pair of lateral epidermal depressions that are devoid of white spots is found in the region of the anterior intestine, approximately ⅓ of the body length from the anterior end (Fig. 1). We were unable to locate these areas on any of our sectioned material and do not know their function, but they might be nephridiopores.

Body wall, musculature and parenchyma.—The epidermis is 50–56 μm in height, and possesses no unusual features. The dermis is 20–22 μm thick.

Body wall musculature consists of an outer circular layer (12–14 μm thick) and inner longitudinal layer (80–136 μm thick in the anterior region of the intestine). A single layer of crossed, diagonal muscle fibers was found between the circular and longitudinal muscle layers. The longitudinal muscle layer is divided into outer and inner layers, from the region just posterior to the brain, anteriorly (Figs. 3,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4). The outer portion continues as a distinct, compact layer, next to the circular muscles, to the tip of the head. Anterior to the brain, outer longitudinal fibers bend inward to contribute to the proboscis insertion, which is composed primarily of inner longitudinal fibers (Figs. 3, 4). Due to the contribution of the outer layer, musculature forming the proboscis insertion represents a precerebral septum. Inner longitudinal muscle fibers penetrate between the muscle bundles of the septum and continue as head retractors (Figs. 3, 4); thus the septum is of the split condition as defined by Kirsteuer (1974). Dorsoventral musculature is only weakly developed and occurs primarily in the stomach region, with muscle fibers running through the parenchyma in that area.

Parenchyma occurs in limited amount in the precerebral region and in the area between the two longitudinal muscle layers. A thick layer surrounds the proboscis sheath in the brain region, and continues to the intestinal region. Posteriorly a small amount of parenchyma surrounds the dorsal blood vessel. Parenchyma forms a rather thick cushion around the stomach and lateral nerve cords, becoming reduced posteriorly.

Nervous system.—The brain consists of 2 dorsal and 2 ventral lobes, approximately equal in size. The ventral commissure is thicker and shorter than the dorsal one. Neurochord cells were not found. Along the anterior part of the stomach and the anterior intestinal region, the lateral nerve cords send off many nerves to the epidermis (Fig. 5). Posteriorly the 2 lateral nerve cords descend ventrally and medially before joining at the posterior end of the animal. Cerebral organs and eyes are well-supplied with nerves. The proboscis has 10 proboscis nerves (counted in 1 animal, Fig. 6).

Sensory organs and cephalic glands.—The cephalic glands (Fig. 7) extend barely posterior to the ventral commissure, and empty into the frontal organ, as in *Poseidonemertes caribensis* (Kirsteuer, 1974). The frontal organ (Fig. 2) consists of a fenestrated epidermis just dorsal and anterior to the rhynchodaeal pore. The cell bodies of the cephalic glands are primarily found posterior to the cerebral organs but anterior to the brain.

The eyes are large (28 × 24 and 26 × 22 μm diameter, 1 serially sectioned specimen) (Fig. 8) with cup-shaped pigment surrounding a central nervous area.

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Figs. 1–3. *Poseidonemertes collaris.* 1. A, External features showing conspicuous eyes, anterior cephalic grooves, rhynchodaeal opening (dashed oval), posterior cephalic grooves in relation to brain and anterior lateral nerve cords (dashed lines) and pair of lateral depressions (thickened areas along sides); B, Enlargement showing details of head; 2, Frontal section of anterior head region, showing characteristic collar of posterior cephalic tissues resulting from contraction of tip of head; 3, Transverse section of the proboscis insertion or precerebral septum showing contribution of both outer and inner longitudinal muscles to the septum. Muscle bundles of split septum are also depicted.

List of Abbreviations, Figures 1–11: ACG, anterior cephalic groove; AS, accessory stylet sac; B, basis; BR, brain; C, collar; CE, columnar epithelium; CG, cephalic groove; CGL, cephalic glands; CM, circular muscles; CO, cerebral organ; DBV, dorsal blood vessel; E, eye; ES, esophagus; FO, frontal organ; GD, gonoduct; HRM, head retractor muscle; ILM, inner longitudinal muscle; IN, intestine; LBV, lateral blood vessel; LD, lateral depression; LM, longitudinal muscle; LN, lateral nerve; N, nerves; OLM, outer longitudinal muscle; OV, ovary; PCG, posterior cephalic groove; PCS, precerebral septum; PN, proboscis nerve; PR, proboscis; PY, pylorus; RH, rhynchocoel; RM, rhynchocoel muscle; RP, rhynchodaeal pore; RS, rhynchodaeal sphincter; S, stylet; VC, ventral commissure.


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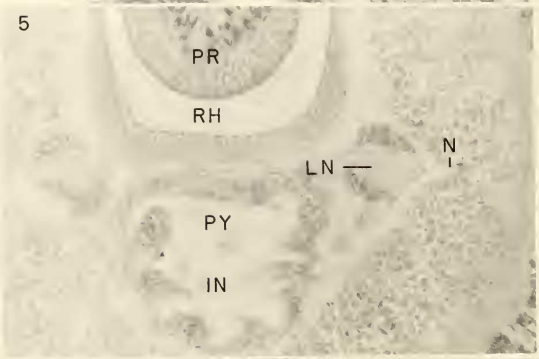
HRM
PCS
ILM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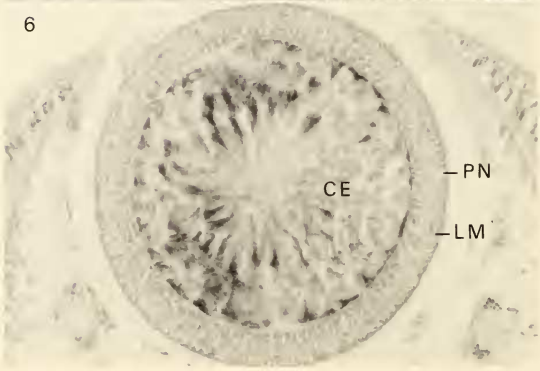
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CE
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The cerebral organs are approximately 100 μm long and extend nearly to the precerebral septum. They are comprised of a median ciliated canal next to and partly surrounded by a more lateral neuroglandular tissue (Fig. 2), and are innervated by nerves that enter at an antero-medial position. The ciliated duct of each organ opens into the anterolateral corners of the anterior cephalic grooves.

Proboscis apparatus.—The large rhynchodaeal pore is subterminal. Anterior to the pore and extending to the tip of the head is a narrow, ventral, ciliated depression. The pore leads into a thin-walled rhynchodaeum. A strong rhynchodaeal sphincter muscle occurs slightly anterior to the proboscis insertion (Fig. 7). The rhynchocoel extends to the posterior end of the animal. Its wall contains 2 distinct muscle layers, an outer, thick circular layer and an inner longitudinal layer lined by thin endothelium. Posteriorly the circular muscle layer becomes much thickened (Fig. 9).

The proboscis is of the typical monostiliferan form. The anterior proboscis chamber is lined by a columnar, glandular epithelium that forms distinct papillae. The musculature is well-developed, and consists of an outer circular layer next to the columnar epithelium, a middle longitudinal layer that is divided into 2 bands by the proboscidial nervous system, and a thin (1–2 fibers) inner circular layer adjacent to a thin squamous endothelium (Fig. 6). The posterior part of the proboscis narrows and consists of columnar epithelium, a thin longitudinal muscle layer and endothelium. The proboscis and continuing proboscis retractor muscles extend approximately ¾ of the length of the animal.

The central stylet lacks ornamentation and averages 87.5 μm in length by 16.4 μm in width at its base (Table 1). In some specimens, the stylet widens in a band anterior to its proximal piece. The basis is longer than the stylet (average length = 119.4 μm, average width = 11.6 μm, Table 1). It is cylindrical in shape, has a slightly indented waist, and is rounded at its posterior end (Fig. 10). In live specimens the posterior ⅓ to ¼ (average = 29%, SD = 0.04, N = 5) of the basis is characteristically more darkly pigmented than the anterior region. Two accessory stylet sacs are present, each with 0 to 4 developing stylets (Table 1, Fig. 10).

Digestive tract.—The esophagus, which is narrow and not highly folded, opens into the anterior end of the rhynchodaeum, anterior to the rhychodaeal sphincter (Fig. 7). The columnar epithelial cells of the esophagus have cilia that are shorter and more sparsely distributed than in the stomach. The esophagus extends posterior to the brain, where it gradually widens and empties dorsally into the capacious, highly folded stomach. Neither the esophagus nor the stomach appears to be highly glandular. Posteriorly the stomach becomes a flattened, non-folded pylorus. The pylorus is lined by non-ciliated cells, and empties dorsally and broadly into the intestine (Fig. 5). The shape of the pylorus is influenced by longitudinal muscles which ensheath the entire foregut.

At the junction of the pylorus and intestine, the intestinal epithelium contains

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Figs. 4–6. *Poseidonemertes collaris.* 4, Frontal section at level of proboscis insertion and precerebral septum, showing contribution of outer longitudinal muscles to septum (arrow) and inner longitudinal muscles continuing as head retractor muscles; 5, Transverse section near pyloric-intestine junction. Section shows nerves to body wall, characteristic throughout anterior intestinal region; 6, Transverse section of anterior chamber of proboscis, showing 10 proboscidial nerves.

Table 1.—Measurements of the stylet apparatus of *Poseidonemertes collaris*.

Animal number	Basis length, μm	Basis width, μm	Central stylet length, μm	Central stylet width, μm	Ratio of central stylet length to basis length	Number of accessory stylets per sac
1	—	—	—	—	—	3, 3
2	100	50	100	—	1.0	2, 0
3	122	25.5	91.8	—	0.75	3, 2
4	137	46	80.5	15	0.59	3, 3
5	115	37	76.5	20.4	0.67	3, 3
6	124.5	27	102	18	0.82	3, 4
7	118	22	74	12	0.63	4, 4
Range	100–137	22–50	74–102	17–20.4	0.59–1.0	0–4
Number	6	6	6	4	6	14
Average	119.42	34.58	87.47	16.35	0.74	2.86
Standard Deviation	12.17	11.59	12.14	36.46	0.15	1.03

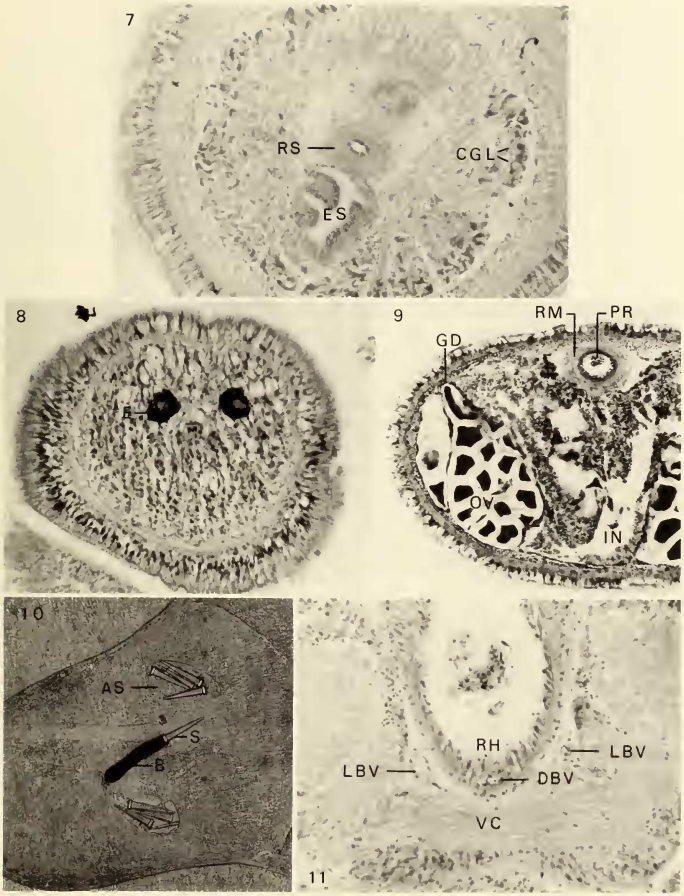
both blue- and red-staining cells, indicating secretory diversity in this area. Both types of cells continue through much of the length of the intestine although the blue-staining cells are far more restricted in distribution, being found mainly in the mid-dorsal lining.

The intestinal caecum is broad and shallowly indented, but without diverticula, and occasionally extends to the posterior end of the brain. The anterior lateral diverticula of the intestine sometimes bend forward and their tips occasionally extend beyond the caecum anteriorly. Lateral intestinal diverticula are often bifurcated and the tips of the bifurcations may branch even more. The anus is terminal.

Circulatory system.—The 2 cephalic blood vessels form an anterior loop behind the eyes at the level of the anterior cephalic grooves, and in the region of the ventral brain commissure they converge with the dorsal blood vessel which runs within the rhynchocoel wall for a short distance (Fig. 11). It could not be determined from our material whether the dorsal vessel joins both or only one of the lateral vessels anteriorly. Posterior to the convergence, the 2 lateral vessels lie above the lateral nerve cords for a short distance, then descend medially to a position ventral to the lateral cords. The blood vessels in the anterior part of living worms lie medial to the lateral nerve cords and can be seen to weave in and out next to the tips of the lateral intestinal diverticula. The dorsal blood vessel is contractile and the blood is colorless. Near the posterior end of the body the 3 vessels appear to unite dorsal to the intestine.

Excretory system.—In the anterior intestinal region is a poorly-defined duct dorsal to each lateral nerve cord that may represent the excretory system, which latter does not appear to be well-developed. Living specimens did, however, display large, lateral, rectangular to oval areas approximately 0.1 to 0.8 mm long (depending on contraction state of the animal) and about ⅓ of the body length posterior to the head which might be nephridiopores (Fig. 1). These areas were not visible on any sectioned material.

Reproductive system.—Sexes are separate. Gonads lie between and ventral to the lateral intestinal diverticula, from close to the anterior end of the intestine to



Figs. 7–12. *Poseidonemertes collaris.* 7, Transverse section at level of rhynchodaeal sphincter just anterior to proboscis insertion. Part of the insertion can also be seen dorsal to sphincter; 8, Transverse section of tip of head showing prominent eyes; 9, Transverse section through posterior region showing ovary, gonoduct, structure of intestinal diverticulum and posterior intestine, and strong circular musculature of posterior region of rhynchocoel wall; 10, Stylet apparatus in partly everted proboscis from living specimen; 11, Transverse section at level of brain, showing dorsal blood vessel within rhynchocoel wall.

the posterior tip of the animal. Both ovaries and testes are arranged in a single row on each side of the intestine, each mature gonad extending from the ventrum to the dorsum of the animal. Gonoducts are dorsolateral (Fig. 9). Mature ovaries typically contain about 25 oocytes, but can contain up to 50 oocytes each.

Remarks on biology.—Specimens were found in the samples we collected most months of the year, although they seemed to be more abundant (or at least easier to locate) during summer months. The animals are rapid burrowers and live in mucus burrows covered with sand grains and other sediment. From observations of the microhabitats where most individuals were collected, these worms seem to prefer sandy mud rather than finer sediments, and tend to occur where there are moderate amounts of algae (primarily ulvoids). They were not found in anoxic mud.

Sexually mature animals were collected in June, July, and August, and one mature female was found in November. One female released eggs in August. The eggs were fertilized with sperm taken from a mature male, and early development was observed. Fertilized eggs are oval, 92 × 112 μm diameter (with fertilization membrane included, 173 × 204 μm in diameter) and are white to barely pink in color. Both unfertilized, but extruded, and fertilized eggs are covered by a thick transparent membrane. Fertilized eggs released swimming larvae within 18 hours in water kept at approximately 60°F. Eyespots became visible by day three. Larvae were of the typical hoplonemertean oval form, except that they were rather depressed dorsoventrally. They were rapid swimmers in comparison to larvae of *Carcinonemertes* species (pers. obs.). Three day old larvae have functioning musculature, as witnessed by the fact that one individual changed its dimensions from 122 × 82 μm to 163 × 61 μm by stretching.

Discussion

Several small, pale, marine, two-eyed monostiliferans have been described from various parts of the world (e.g., *Amphiporus bioculatus, Correanemertes bioculatus* and *Poseidonemertes gondwanae* as discussed in Kirsteuer (1967); *Paranemertes biocellatus* Coe, 1944; *Tetrastemma worki* and *T. hansi* as discussed in Corrêa (1961); *Poseidonemertes caribensis* Kirsteuer, 1974). The animals described in this paper superficially resemble many of the above worms. The arrangement of musculature in the anterior body region, however, places the present specimens firmly within genus *Poseidonemertes.* Kirsteuer (1974) provided diagnostic descriptions of several nemertean genera with split longitudinal musculature. The genus *Poseidonemertes* is characterized by members having split longitudinal musculature, with contributions from both outer and inner layers forming the proboscis insertion. Due to the contribution of the outer layer, the insertion represents a precerebral septum, which in this genus is characteristically split into muscle bundles (Kirsteuer 1974). Inner longitudinal muscle fibers continue past the septum as head retractors (Kirsteuer 1974). In addition, other features, such as musculature of proboscis sheath consisting of separate layers, rhynchocoel having no appendages and extending into the posterior part of the body, presence of intestinal caecum, lack of extracerebral blood vessels, cerebral organs being anterior to the brain and the dioecious condition of the animals agree with the generic diagnosis for *Poseidonemertes,* as defined by Kirsteuer 1974. Some of our

specimens did show diagonal body wall musculature and thus differ from the generic diagnosis of *Poseidonemertes.* However, the single-fiber layer of diagonal musculature can be easily overlooked. Since this was the only minor generic feature in which our specimens differed from other described *Poseidonemertes,* we consider our specimens to belong to the genus *Poseidonemertes.*

Three species of *Poseidonemertes* have previously been described, all from tropical waters (*P. gondwanae* Kirsteuer, 1967; *P. caribensis* Kirsteuer, 1974; *P. bothwellae* Gibson, 1982). The present animals differ from the other members of *Poseidonemertes* in sufficient features to warrant recognizing them as a new species. The differences include the following: The sharply pointed, elongated head, as well as the characteristic contracting of the tip of the head into more posterior parts of the head, forming a collar of tissue around the tip, are apparently unique among described members of the genus *Poseidonemertes.* However, the ability to retract the head is not unusual among amphiporids (Jon Norenburg, pers. comm.); similar behavior was described by Coe (1904) for *Paranemertes californica,* and Berg (1972) for *Nipponnemertes pulcher.* The head of *P. gondwanae* is pointed, but the cephalic grooves of that species are not prominent, nor does the animal retract the head tip back to the grooves (Kirsteuer 1967). In the other two species the head is rounded (Kirsteuer 1974; Gibson 1982), and in disturbed animals of *P. caribensis* the head widens posterior to its tip (Kirsteuer 1974), a behavior much different from that observed in the present animals. The presence of lateral depressions approximately ⅓ the body length posterior to the anterior end, as occurs in the California animals, has not been described for other species of *Poseidonemertes.* In addition, the numerous nerves leading from the lateral nerve cords to the body wall in the anterior intestinal region in *P. collaris,* have not been described for other species of the genus. The lateral gut diverticula of *P. collaris* are at least bifurcate and may show even more branching; lateral gut diverticula are missing in *P. bothwellae* (Gibson 1982) and are unbranched in *P. gondwanae* and *P. caribensis* (Kirsteuer 1967, 1974), and in *P. caribensis* the intestinal caecum is provided with branches (Kirsteuer 1974).

Poseidonemertes collaris differs from the previously described species in other ways as well. In *P. gondwanae* the stylet is nearly as long as the basis, the basis is truncated, the dorsal blood vessel does not enter the rhynchocoel wall, and *P. collaris* averages twice the length of *P. gondwanae* (Kirsteuer 1967). In *P. caribensis* the proboscis sheath does not extend to the posterior end of the body (Kirsteuer 1974). Specimens of *P. bothwellae* are dark brown in color, and the dark color obscures the four eyes in living animals (Gibson 1982). In addition, whereas the stylets of the Australian and Californian specimens are similar in size, the stylet basis in the new species is approximately twice the length of that for *P. bothwellae* (Gibson, 1982).

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